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THE MICROVASCULAR NETWORK OF THE CAUDAL PART OF THE TRUNK AND OF THE CAUDAL FINS OF THE DOLPHIN

UNEDITED TRANSLATION
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by

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The circulatory bed of the dolphin's skin fulfills a number of /42* functions. Besides its basic function of maintaining the vitality of all cells and tissues, the circulatory system in aquatic animals is involved in (a) temperature regulation [A.G. Tomilin, 1951] and in (b) the creation of conditions favorable for locomotion in an aquatic environment. First of all, dolphins possess "special vascular organs" [S.V. Pershin, A.S. Sokolov, and A.G. Tomilin, 1970 and 1974], which provide the fins with elasticity and provide hydroelasticity when the animal is in motion. Secondly, dolphins possess dermal discharges [G.G. Tinyakov, V.P. Chumakov, and B.A. Sevast'yanov, 1973; E.T. Uskova and L.N. Mamot, 1975], whose origin must be sought in the animal's microcirculatory processes. As one might expect, these discharges moisten the skin, making it possible for the animal's body to glide through the water more easily.

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* Translator's note: Numbers in the right-hand margin refer to the corresponding page in the Russian text.

An investigation has been carried out on the insulated caudal fins and the adjoining section of the trunk of the common dolphin (Delphinus delphis) and of the harbor porpoise (Phocaena phocaena). Material for this investigation was provided by Prof. G.B. Agarkov.[1] Two macropreparations were utilized in order to inject the vessels with radiopaque substance; skin and the fascial covering of the tendons (peritendineum) were taken from three caudal fins in order to show the microvessels on micropreparations by means of the silver impregnation method [V.V. Kupriyanov, 1965]. /43

Study Results

X-ray photographs of the vessels of the caudal fin (Figure 1) show the arterial branches of the medial caudal artery. They extend along the middle of the right and left lobes, repeatedly sending out secondary branches towards the outer zones. Their location corresponds to a concentration of connective tissue between the two cutaneous plates that form the caudal fin. The terminal branches at the level of the arteriolae penetrate into the subcutaneous fat and enter into the papillae of the skin itself, or derma (corium). Thus, they appear very close to the surface of the skin and provide nourishment for the epidermis. The anatomy of the blood vessels of the dolphin's caudal fin is very well described in the work of S.V. Pershin, A.S. Sokolov, and A.G. Tomilin [1974]. More will be said of this matter further on. It is important to note that there is no strict segmentation in the lobes of the caudal fin and, as a consequence, the diverging arterial branches are distinguished by size.

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[1] For which I shall take this opportunity to thank him.

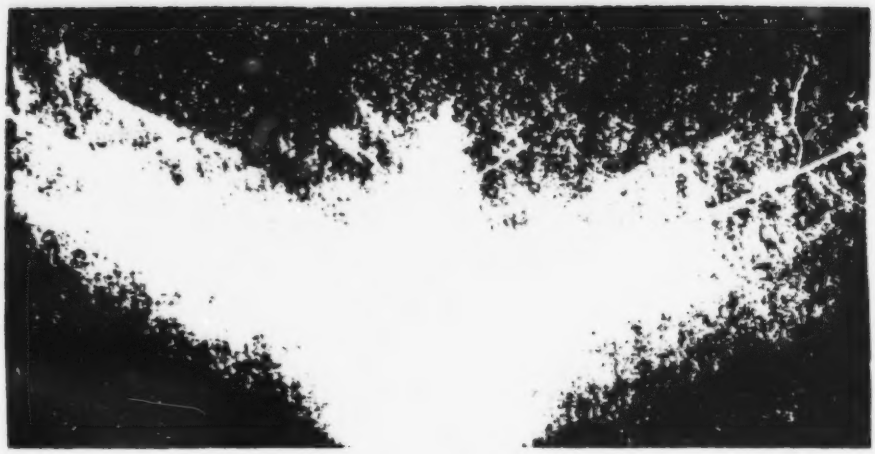

Рис. 1. Артерии хвостового отдела туловища и хвостового плавника дельфина
Рентгенограмма.

Fig. 1. Arteries of the dolphin truncal caudal part and the caudal fin
Roentgenogram

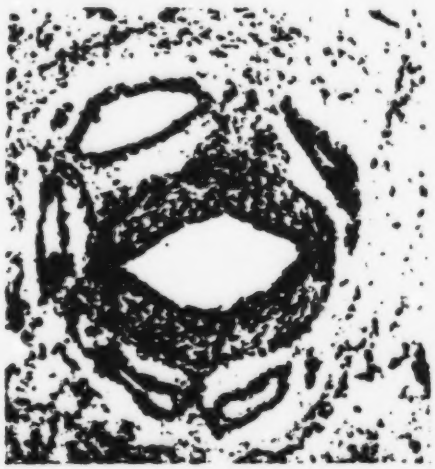

Рис. 2. Комплексные сосуды в тканях хвостового плавника дельфина обыкновенного (мышечная артерия и 6 вен)
Инъецированная серебром. Мацерат

Fig. 2. Complex vessels in tissues of D. delphin caudal fin (muscle artery and 6 veins)
Silver impregnated. Macerat

The surrounding veins (Figure 2) are a characteristic feature of the primary and secondary arterial branches that diverge outward from the caudal fin. This area displays an unusual pattern of multitrunk accompaniment to a common artery of the muscle type. As opposed to the thick (muscular) central layer, the outer layer of the artery is thin and immediately adjacent to it are venous trunks in the walls of which the muscular elements are poor. Similar relationships among the arteries and veins in the caudal fin of the dolphin were first described by A.G. Tomilin [1951] and the term "complex vessels" was proposed as their designation. The functional significance of these complex vessels have been subjected to special scrutiny in many works by V.E. Sokolov, A.G. Tomilin, and S.V. Pershin.

The complex vessels are not encountered at the level of the microcirculatory bed. In the fascial-tendinous plate separating the hypoderm from the loose connective tissue in the mass of the lobes, through which the main vessels pass, the microangioarchitectonics* are characterized in theory by the very same parameters as in the fasciae and aponeuroses of the human body. A typical triad is clearly seen in Figure 3: the terminal artery is accompanied as it passes along by two comites. The presence of muscular cells in the vein walls and even in the wall of the venules that enter them is worthy of note. The capillary bed is of ordinary density; as a rule, the cells of the cpillary network are polymorphic. Figure 4 shows the numerous arteriolovenular anastomoses in the peritendineum along the path of the tendon.

The capillary loops at this point have a rectangular shape. /44
The venules are thin-walled; their width is relatively great and

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* Translator's note: This is a literal translation of the Russian mikroangioarkhigektonika.

Рис. 3. Фрагмент микроциркуляторного русла в фасциально-апоневротической выстилке кожи дельфина.
Импрегнация серебром. Ув. 100

Fig. 3. Microcirculatory bed in the fascial-aponeurotic lining of the dolphin skin (a fragment).
Silver impregnation. Magn. 100

Рис. 4. Микрососудистая сеть в перитендинии по ходу сухожилия в хвостовом отделе тела дельфина.
Видны артериоловенулярные анастомозы. Импрегнация серебром. Ув. 100

Fig. 4. Microcirculatory bed in the peritendineum along the course of tendons in the dolphin truncal caudal part.
Arteriolo-venular anastomoses are seen. Silver impregnation. Magn. 100

exceeds the diameter of the capillaries by a factor of 8-10. The arteriolovenular index is 1:5. Arteriolovenular anastomoses are almost equal in diameter to the arterioles. The existence of these /45
anastomoses gives a special character to the capillary and vascular network, not to mention the fact that they are also responsible for fundamentally changing the microcirculation of the blood in the lobes of the dolphin's fins.

The fusion of postcapillaries in places where adipose cells are localized results in the formation of tiny lacunae 100 X 150 mμ in size (Figure 5).

An exceedingly convincing confirmation of the active role of the dolphin's circulatory system in temperature regulation and in the creation of a hydroelastic effect is the structure of the microcirculatory bed on the boundary between the papillar layer of the dermis and the epidermis. The papillae of the dermis have an atypical structure. They are actually continued over a considerable distance in the form of rodlets or tubules in the adjacent layer of the epidermis. A picture of a "channelized" epidermis appears in cross sections of the dermis and epidermis (Figures 6 and 7). The borders along the tubules are formed by cells of the ectodermal epithelium, whose content is the interstitium of the corium. Cellular shapes have not been found within the tubules, but the circulatory capillaries that pass through can be observed. They are accompanied by the basic matter of the connective tissue, usually rich in glycosaminoglycans. Near the surface of the skin the tubules end blindly. A unification of neighboring tubules is observed.

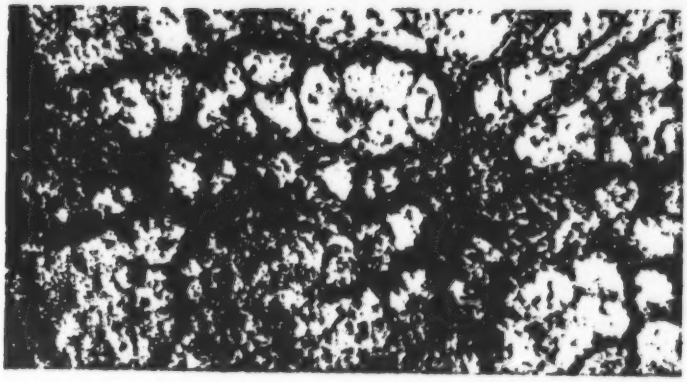

Рис. 5. Место слияния венул в сосочковом слое дермы дельфина обыкновенного.

Образование венозного расширения (лакуна). Импрегнация серебром. Ув. 48

Fig. 5. Place in the papillar layer of the dolphin dermis where the veins fuse.

Formation of the venous dilatation (lacuna). Silver impregnation. Magn. 48.

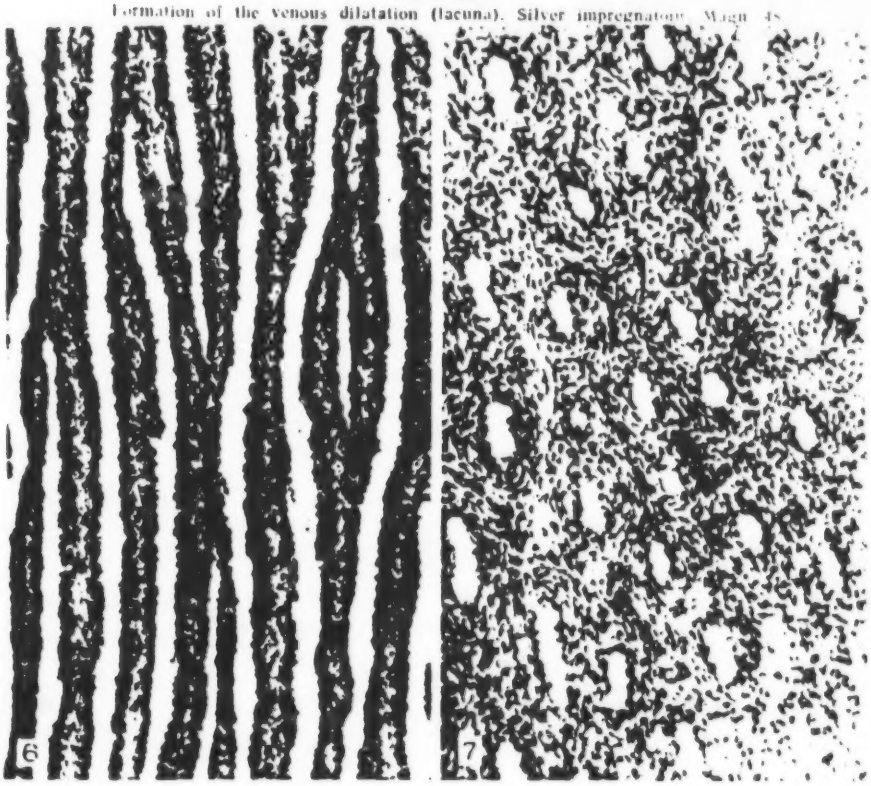

Рис. 6. Эпидермис хвостового плавника дельфина обыкновенного, покрытого [illegible] длинными сосочковыми корнями (волосяные [illegible])

[illegible] Импрегнация серебром. Ув. [illegible]

Fig. 6. Epidermis of the dolphin caudal fin covered with long papillae [illegible] (vestigial hairs)

[illegible] Silver impregnation. Magn. [illegible]

Рис. 7. Кожа дельфина [illegible] что и на рис. 6

[illegible] Импрегнация серебром. Ув. [illegible]

Fig. 7. The dolphin skin [illegible] as on Fig. 6

[illegible]

Discussion

The interest in vascularization of the dolphin's skin is quite understandable. A mammal's life in the water and its need to breathe air are phenomena that are difficult to combine. The need to provide for the oxygen exchange to tissues is extraordinarily great under such conditions. Dolphins must renew their air supply approximately every two minutes.

The medial caudal artery[1] is the main pathway for carrying blood to the caudal part of the dolphin's trunk. It passes ventrally from the vertebral column and it is accompanied by veins of the same name. Right and left branches diverge from the main artery towards the lobes at the level of the middle of the caudal section of the vertebral column and these provide the supply of blood to the microcirculatory bed.

There is no agreement among specialists regarding the composition of the arterial tree in the dolphin body. As far as the pathways of the venous drainage are concerned, there are a number of vague viewpoints. First of all, dolphins do not possess a division of veins into deep and superficial. The principle of paired deep comites gives way in the dolphin's case to the principle of multitrunking. According to A.G. Tomilin [1951], the complex vessels are one artery and a number of accompanying veins—up to 10 or even 20 in number according to S.V. Pershin, A.S. Sokolov, and A.G. Tomilin [1970]. They are supplemented by individual veins that do not duplicate the path of the arteries. Nature took great pains to ensure the venous drainage of the blood. This should not be understood to constitute proof of the

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[1] In the International Veterinary Anatomical Nomenclature this is the central caudal artery.

vulnerability of the arterial blood flow. When we talk of the main [trunk] arteries, there is no doubling in the case of the dolphin and /47
no loose type of arterial passages. But there is an indirect arterial blood flow in the bodies of dolphins. It is performed by plural anastomotoses of the segmentary arteries of the body, including [those] at the level of the microcirculatory bed. The very same thing should be said of the connected arterial secondary branches in the tissues of the caudal lobes. But if one lobe artery is put out of action due to the absence of mainline collaterals, the microanastomoses cannot compensate for it.

Statements relative to the distribution of microvessels in the subcutaneous interlayer and in the skin of dolphins justifiably stir up controversy. The absence of muscles in the lobes of the fins cause the dermal plates of the fins to appear to be separated only by the fascial-tendinous membranes, between which are located the distributative and collecting vessels, which are in turn surrounded by loose connective tissue. The tendinous rodlets, disintegrating under the skin on the plates, are themselves equipped with an "aponeurotic sheath" [G.B. Agarkov, B.G. Khomenko, and V.G. Khadzhinskii, 1974]. We can assume that this sheath is most likely fascial; it has an external, more compact, fibrous layer and an inner layer that adjoins the tendon--a loose one that suggests the synovial layer of tendon sheaths, or at least the peritendineum. A dense microvascular network is found here.

Yu.F. Yatsenko [1975] had made a thorough study of the distribution of blood vessels in the skin of the dolphin's head. His conclusion regarding the identical distribution of blood vessels in the skin of dolphins and in the skin of terrestrial mammals cannot be accepted in order to evaluate the vascularization of the skin of the

dolphin's fins. Thus, the author has calculations to report that are contrary to the commonly accepted findings regarding a reduction in the size of the passages bringing blood to the capillary bed and a growth in size over the distance from the capillaries to the veins. The diameter of the dermal arterioles, in his opinion, varies within 8 to 13 mμ, while the diameter of the venules varies from 14 to 19 mμ. Furthermore, the diameter of the adducting knee in the capillary loop of the dermal papilla is equal to 25-35 mμ according to the author, while the diameter of the abducting knee is twice as great. Consequently, it turns out that the capillaries that branch out from the arterioles are three times larger than the parent trunk. The venule that forms as a result of the fusion of the postcapillaries proves to be narrower. A similar relationship of sizes in the metabolic vessels prevent normal microhemodynamics in the skin.

In any case, the richness of the dermal vascularization in the fins of cetaceans is not open to doubt. P. Scholander and W. Schewill [1955], K. Schmidt-Nelsen [1972], and S.V. Pershin, A.S. Sokolov, and A.G. Tomilin [1974] are among those who have written on this subject. A similar picture is to be found in the flippers of seals [A.S. Sokolov, 1959; A. Magomaev, 1975], in which a multitude of arteriolovenular anastomoses of the glome type (epitheloid)--up to 900 per cm^2--have been found directly under the epidermis. Anastomoses of this type have not been found in the skin of dolphins [G. Molyneux and M. Bryden, 1975].

A detailed description of the epidermis of cetaceans, including a species of dolphin, was presented in 1955 by V.E. Sokolov. The long dermal papillae in the epidermis that he described and drew are fully

confirmed by my photographs, although they were made from preparations of other species of dolphins. According to V.E. Sokolov, the dermal papillae enter into the cells of the base of the epidermis and extend throughout its entire thickness to the horny layer perpendicular to the surface of the skin. The author believes that the papillae create ideal conditions for the transfer of heat through the capillaries. In another work [V.E. Sokolov, 1965], the same author presents some /48 measurements of the epidermis of Black Sea dolphins. It appears that the length of the dermal papillae reaches 1.37 mm in the bottlenose dolphin [Tursiops truncatus]. The thickness of the horny layer--the lucid layer is lacking--amounts to not more than 0.1 mm (a total of only 4.2% of the thickness of the epidermis). Clearly, the emergence of heat onto the surface of the skin and dermal discharges from the papillae are greatly facilitated.

In 1973 G.G. Tinyakov, V.P. Chumakov, and B.A. Sevast'yanov found blood vessels in the skin of the sperm whale [Physeter catodon] at the base of the papillae of the dermis. The center of the papilla was also occupied by a vessel that was 60 mμ in diameter. The authors expressed the opinion that fatty emulsion is transported along this vascular tubule to the epidermis. V.G. Dargol'ts, E.V. Romanenko, and V.E. Sokolov [1978] rejected the hypothesis of G.G. Tinyakov, V.P. Chumakov, and B.S. Sevast'yanov. An experimental verification of the hypothesis had not been made. All the same, G.G. Tinyakov's observations deserve attention. The material that I have studied suggests that the epidermis in the skin of the dolphin's fins is pierced by numerous rodlets of the dermis that can be provisionally called tubules. In fact, their diameter varies between 40 and 60 mμ.

G.G. Tinyakov and his colleagues assumed these tubules to be blood vessels. In actual fact, a vessel of the capillary type is located in the tubule itself, surrounded by interstitial gel. This is nothing other than an extension of the papillary layer of the dermis in the epidermis [G.B. Agarkov, 1974]. The supposition that fatty emulsion passes along this interstitial tubule hardly corresponds to reality. In the first place, it is necessary to consider the fact that a blood capillary follows along the tubule. Given a thickness of 3-4 mm, the epidermis of the skin of the dolphin's fin could not be effectively supplied with nourishment from the vessels of the dermis adjacent to the base of the epidermis. The radius of diffusion would be unusualy large (up to 4000 mμ). Even if the capillaries in the interstitial tubule in the epidermis did not reach as far as the surface layers, its very presence improves conditions for nourishing the cells. But the purpose of this particular construction of the epidermis is not solely to provide more favorable microcirculation: due to the presence of tubules with the capillaries passing through them and containing interstitial fluid, it is possible to regulate the turgor of the skin and thus to permit an even greater hydroelastic effect to be achieved.

The matter of surface dermal discharges in dolphins has not been studied. It is considered that since the skin of these animals does not have sudoriferous, nor sebaceous, nor even muciparous glands with their efferent ducts, there can be no question of any kind of dermal discharges. The observations of G.G. Tinyakov, V.P. Chumakov, and B.A. Sevast'yanov [1973], however, provide grounds for a different interpretation. Special research became necessary. As a result of this, the work of E.T. Uskova and L.N. Mamot [1975] has proved

valuable. These authors had set themselves the task of verifying the chemical composition of the liquid medium on the surface of the dolphin's skin and of studying the physical properties of this medium. They became convinced that biopolymers are discharged through the epidermis together with detached and degenerated cells of the epithelium. It also turned out that the dermal discharges of the dolphin have the ability to lower frictional resistance.

An analogue of such material can be found in the mucous discharges in the scale covering of bony fishes. These discharges behave like weak solutions of biopolymers that lower the turbulent frictional resistance by 30-40% in comparison to the resistance of the water [S.F. Manzii and K.P. Mel'nik, 1978].

The results of the studies that I have conducted make it possible to provide an approximate answer to the question of how the /49
discharge of such nonstandard "lubricating" matter occurs (Figure 8). The basic matter of the connective tissue of the derma with the lipoproteins and proteoglycans that it contains passes from the papillary layer into the tubules described above, piercing the epidermis and representing an extension of the papillae. Blood plasma from the capillaries of the papilla exude through them. It is quite possible that the cells of the epidermis surrounding the tubules of the derma have the ability to secrete biopolymers that connect up with the contents of the tubules. The accumulation of fluid in the tubule precedes its discharge onto the surfce of the skin through the horny layer of the epidermis. While the body and fins are in motion, the relief of the skin changes and the amount of discharge increases. A /50
final answer to the question regarding the mechanism of dermal discharges in dolphins can only be provided by further research.

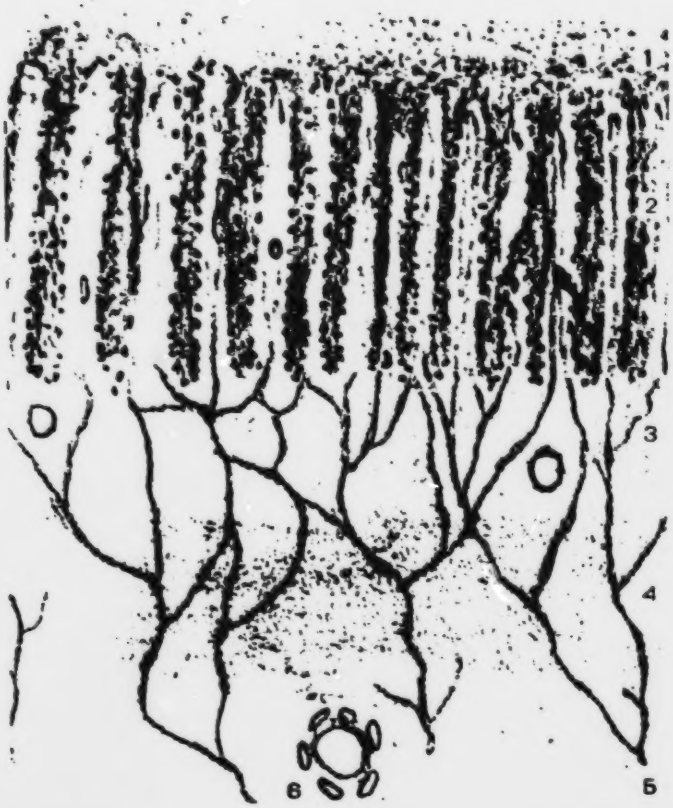

Рис. 8. Реконструкция микрососудистой сети кожи дельфина (схема)

1 — [illegible] эпидермиса, 2 — [illegible] сосочков, 3 — [illegible] сосочковый слой дермы, 4 — [illegible] сетчатый слой дермы, 5 — [illegible] сосудистое [illegible], 6 — [illegible]

Fig. 8. Reconstruction of the microvascular network of [illegible] dolphin skin (a scheme)

1 — [illegible] layers of the epidermis; 2 — [illegible] layers; 3 — [illegible] canaliculi; 4 — papillae; 5 — [illegible] layer of the dermis; 6 — [illegible] vessels; 5 — vascular layer of [illegible]

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MICROVASCULAR NETWORK IN THE CAUDAL PART OF THE DOLPHIN BODY AND IN ITS CAUDAL FINS

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The medial caudal artery, being a continuation of the aorta, ensures blood transport to all tissues of the caudal part of the dolphin body and its caudal fins. The branches of this artery are accompanied with some veins (complex vessels). In the microcirculatory bed there are many arteriolo-venular anastomoses. The greatest attention of the author has been paid to the capillaries of the dermal pappilae which deeply penetrate into epidermis. It is possible to think that in this way: a) thermoregulation is improved; b) a greater hydroelastic effect is reached; c) epidermis blood supply is facilitated; d) certain conditions are created for synthesis of the dermal excretion.

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